

Interaction between *Halobatrachus didactylus* and *Anguilla anguilla*: What happens when these species occur in sympatry?

by

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ABSTRACT. - The Lusitanian toadfish, *Halobatrachus didactylus*, and the European eel, *Anguilla anguilla*, are benthic fish species, which occur in sympatry in the southern Iberian Peninsula and north-west Africa. The consequences of this sympatry were evaluated through the analysis of distribution, abundance and feeding ecology of both species in the Mira estuary, a small system located on southern Portugal. A total of 1734 toadfish and 196 eels were caught with a beam-trawl in six sampling areas covering the entire estuary. Both species showed burrowing habits and a high diet overlap. The dominance and voracity of the toadfish, which includes glass and yellow eels in its diet, may contribute to explain the spatial segregation between the species, with eels occupying peripheral areas upstream (freshwater and upper estuary) and downstream (*Zostera* spp. beds near the sea). This spatial segregation reduces habitat availability for eels, which may have serious consequences on a population already subjected to an important loss of habitat due to anthropogenic causes. If this situation results from the interaction between the two species, it may become even more unfavourable to eels because subtropical species like the Lusitanian toadfish may spread northward as a result of raising temperatures caused by climate change.

RÉSUMÉ. - Interactions entre le poisson crapaud *Halobatrachus didactylus* et *Anguilla anguilla* : qu'arrive-t-il quand ces espèces sont en sympatrie ?

Le poisson crapaud, *Halobatrachus didactylus* (Bloch & Schneider, 1801) et l'anguille européenne, *Anguilla anguilla* (Linnaeus, 1758), sont des poissons benthiques qui vivent en sympatrie dans le sud de la péninsule ibérique et le nord-ouest de l'Afrique. Les conséquences de cette sympatrie ont été évaluées par l'analyse de la distribution, l'abondance et l'écologie alimentaire des deux espèces dans l'estuaire de la Mira, un petit cours d'eau du sud du Portugal. En tout, 1734 poissons crapauds et 196 anguilles ont été capturés au chalut à perche dans six zones d'échantillonnage réparties sur l'ensemble de l'estuaire. Les deux espèces avaient des habitudes d'enfoncement et de fortes similitudes de leurs régimes alimentaires. La dominance et la voracité du poisson crapaud, dont le régime comprenait des anguilles, contribue peut-être à expliquer la ségrégation spatiale entre les deux espèces, les anguilles occupant le système amont (eaux saumâtre et douce) et aval (habitats à *Zostera* spp.). Cette ségrégation spatiale réduit la disponibilité des habitats pour les anguilles et pourrait avoir de sérieuses conséquences sur une population qui subit déjà un fort déclin pour des raisons anthropiques. Dans l'hypothèse où la ségrégation spatiale résulterait de l'interaction entre les deux espèces, la situation pourrait devenir encore plus défavorable pour les anguilles puisque la distribution des espèces subtropicales, comme le poisson crapaud, pourraient s'étendre vers le nord à la faveur du réchauffement climatique.

Key words. - Batrachoididae - Anguillidae - *Anguilla anguilla* - *Halobatrachus didactylus* - Lusitanian toadfish - European eel - Portugal - Mira estuary - Spatial segregation - Trophic relations.

The Lusitanian toadfish, *Halobatrachus didactylus* (Bloch & Schneider, 1801), is a relatively sedentary benthic fish often buried in soft sediments or concealed in rock crevices (Roux, 1986; Bauchot, 1987). Its head and mouth are very wide and the body is robust and quite large, reaching more than 500 mm in total length (Costa, 2004). The species is typical of the Eastern Atlantic subtropical realm occurring from Cabo da Roca (central Portugal) to the Gulf of Guinea (Costa and Costa, 2002). Despite being mainly a marine lit-

toral species, the Lusitanian toadfish is secondarily adapted to brackish water systems in the northern region of its distribution area due to environmental constraints to offspring development (Costa and Costa, 2002; Costa *et al.*, 2003). More active during the night (Campos, 2007), it is a voracious predator (Cárdenas, 1977; Costa *et al.*, 2000) and, as a consequence, these brackish water populations have major impacts on biological communities, especially in small systems (Costa, 2004).

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The European eel, *Anguilla anguilla* (Linnaeus, 1758), is a catadromous fish that spawns in the Sargasso Sea and colonises a wide range of habitats in Europe and North Africa (Tesch, 2003; Domingos *et al.*, 2006). After arrival in brackish water, the young eels show great variability in further movements (Feunteun *et al.*, 2003). With some exceptions (Laffaille *et al.*, 2003), the typical pattern is that large numbers of specimens remain in the middle of estuaries and density gradually decreases up the river, because the influx of glass eels declines with distance from the estuary (Costa *et al.*, 1993; Naismith and Knights 1993; Costa *et al.*, 2008). Generally, eel density is also reduced near the sea as only a small proportion of ascending glass eels remain in that region (Tesch, 2003; Costa *et al.*, 2008). Apparently, the scarcity of eels in the lower reaches of the river basins and in the adjoining seas is related to the avoidance of predators and competitors for space and food, which are usually abundant in more saline areas but decrease sharply upstream (Moriarty, 1987). During the continental phase, the European eel exhibits burrowing habits and feeds mainly on benthic invertebrates and fishes (Costa *et al.*, 1992), being more active at night (Tesch, 2003). Although its narrow and elongated body may extend over 1 m (Tesch, 2003), in estuarine systems the total length is usually less than 500 mm (Costa *et al.*, 2008).

Because *H. didactylus* and *A. anguilla* have similar habits and are sympatric in estuaries and open coastal lagoons of southern Portugal, the aim of this work was to analyse the potential ecological consequences of such sympatry considering the Mira estuary as a case study. With that purpose, the feeding habits and the distribution and abundance of both species along this system were analysed in order to determine if the presence of the Lusitanian toadfish may influence the pattern of colonisation of continental waters by the European eel as well as its trophic ecology.

MATERIALS AND METHODS

Study area

The Mira estuary is located in the south-west coast of Portugal and extends between Vila Nova de Milfontes at the mouth and Odemira at its upper limit (Fig. 1). It is a narrow trench-shaped system, with a length of 32 km and a mean depth of about 6 m (Andrade, 1986). Water temperature ranges between 8.0°C and 26.5°C in the upper reaches and between 12.0°C and 22.5°C in the lower reaches (Costa *et al.*, 1994). Salinity variation is greater in the middle estuary and sediments are usually dominated by mud and/or fine sand, except in both ends of the system where coarse sediment particles predominate (Andrade, 1986). Near its mouth this estuary presents ecologically important eelgrass beds of *Zostera marina* (Linnaeus, 1758) and *Z. noltii* Hornemann,

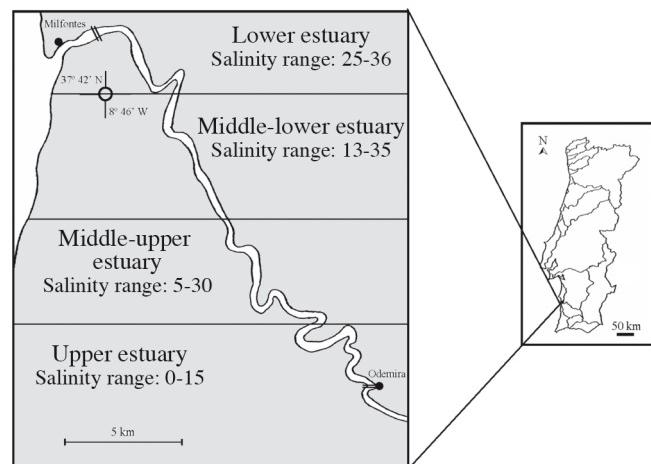


Figure 1. - Study area and zonation of the Mira estuary. Salinity ranges within each zone are also presented. [Zone d'étude et zonation écologique de l'estuaire de la Mira. La salinité de chaque zone de l'estuaire est présentée.]

1832 in the subtidal and intertidal areas, respectively (Almeida, 1988, 1994). It is a well preserved estuary with reduced fishing activity (Almeida *et al.*, 1997). Although other fish species show important populations in this system, like *Solea solea* (Linnaeus, 1758), *Diplodus vulgaris* (Saint-Hilaire, 1817), *Liza ramada* (Risso, 1810) and *Chelon labrosus* (Risso, 1826), *A. anguilla* and *H. didactylus* constitute the top predators in its fish community (Costa, 2004).

Sampling

Fish were caught monthly in two different periods. The first data series was obtained between February 1984 and July 1985 and the second one between July 1991 and May 1993. Sampling was conducted in the morning, during the ebb tide, with a beam-trawl (width \approx 1.5 m; mesh size of 10 mm), which is considered an adequate technique for estimating abundance of *A. anguilla* and *H. didactylus* (Costa, 2004; Costa *et al.*, 2008). Fishing operations were conducted in four different zones covering the entire estuary (Fig. 1). In the lower estuary fishing was performed in three different habitats covering bare sediments and *Z. marina* and *Z. noltii* beds. Therefore, a total of six sampling areas was considered in this study. A variable number of transects was conducted in each sampling area on each sampling occasion but the total surface covered in each transect was registered to estimate the density of both species.

Laboratory procedures

After sampling fishes were frozen until further analysis. In the laboratory, specimens of *A. anguilla* and *H. didactylus* were counted, measured (TL = total length in mm), and dissected to remove their digestive tracts. The stomach and intestine contents were examined under a dissecting microscope, sorted and identified to major prey groups. All food

items were counted and wet-weighted to the nearest 0.001 g.

Data analysis

Data from both periods were pooled because no major differences in the Mira estuary fish community were detected between those years (Costa *et al.*, 1987, 1994). Considering the 228 conducted transects, mean density values (number of fish caught per area swept by the beam-trawl) of *A. anguilla* and *H. didactylus* were computed for each one of the six sampling areas. To study the variability in the abundance of both species along the estuary those values were compared for each species by means of analysis of variance (ANOVA) (Sokal and Rohlf, 1995). Distributions of the species along the estuary were compared by applying the Spearman correlation test (Siegel and Castellan, 1988) to mean densities in each area.

A preliminary analysis of the trophic data revealed that the occurrence, numeric and weight frequencies of major prey groups were highly correlated for each species (Spearman correlation tests, $p < 0.001$). Therefore, to avoid redundancy, diet characterization of both species was based only on the index of occurrence, computed according Hyslop's (1980) formula:

$$IO_i = (S_i/S_c) \times 100$$

where S_i and S_c are the number of digestive tracts with the i^{th} major prey group and the total number of digestive tracts with contents, respectively. The R x C independence G-test with Williams' correction (Sokal and Rohlf, 1995) was applied to the absolute frequencies of occurrence of these prey groups in order to know whether the consumption of such organisms varied between the species.

To determine the dietary overlap between the species the Horn index was computed according to the following formula given by Krebs (1989):

$$HI = [\sum (p_{ij} + p_{ik}) \ln (p_{ij} + p_{ik}) - \sum p_{ij} \ln p_{ij} - \sum p_{ik} \ln p_{ik}] / 2 \ln 2$$

where p_{ij} and p_{ik} represent the proportion of each prey group

Table I. - Density (ind.ha^{-1}) of *Halobatrachus didactylus* and *Anguilla anguilla* along the Mira river basin (mean values \pm standard error). ⁽¹⁾ Excluding freshwater specimens; ⁽²⁾ According to Beja and Magalhães (1995). [*Densité (ind.ha^{-1}) d'*H. didactylus et d'A. anguilla le long du bassin versant de la Mira (moyennes \pm écart-type)**. ⁽¹⁾ A l'exclusion des spécimens d'eau douce ; ⁽²⁾ Selon Beja et Magalhães (1995).]

Sampling areas	<i>H. didactylus</i> N = 1734	<i>A. anguilla</i> N = 196 ⁽¹⁾
Lower estuary – <i>Z. noltii</i> beds	1.1 ± 1.1	47.0 ± 9.5
Lower estuary – <i>Z. marina</i> beds	29.0 ± 8.6	13.5 ± 6.6
Lower estuary – bare sediments	80.5 ± 15.0	0.0 ± 0.0
Middle lower estuary	99.5 ± 17.0	1.7 ± 0.1
Middle upper estuary	79.8 ± 21.6	2.2 ± 0.1
Upper estuary	5.6 ± 3.9	5.1 ± 0.2
Freshwater ⁽²⁾	0.0	> 190.0

in the digestive tract contents of species j and k, respectively. This index ranges between 0 and 1 and significant dietary overlap is considered to occur only when values are higher than 0.60 (Wallace and Ramsey, 1983).

Because *H. didactylus* specimens show important shifts in their diet when they reach around 50 mm and 170 mm (Costa, 2004), all diet analyses were conducted for the whole population and separately for the following length classes: $TL < 50$ mm; $50 \text{ mm} \leq TL \leq 170$ mm; $TL > 170$ mm. For *A. anguilla* these analyses were only performed for the entire population due to the limited number of eels that contained food in their digestive tracts.

RESULTS

Both *Halobatrachus didactylus* ($F = 12.80$; $df = 5, 222$; $p < 0.001$) and *Anguilla anguilla* ($F = 12.96$; $df = 5, 222$; $p < 0.001$) showed significant differences in their abundance along the Mira estuary. However, their patterns of distribution were quite different from each other (Tab. I) and the abundance of both species was negatively correlated ($r_s = -0.89$; $N = 6$; $p < 0.05$). The density of the Lusitanian toadfish was highest in the middle-lower estuary and decreased towards both ends of the system, in contrast to the density of the European eel which increased in an upstream direction, and especially in freshwater. In the lower estuary *A. anguilla* was only present in *Zostera* spp. beds, where *H. didactylus* was less abundant. Glass eels comprised only 26.2% of eels caught in these estuarine vegetated areas.

Although this study indicates that *A. anguilla* and *H. didactylus* may occasionally prey upon other type of organisms their diet in the Mira estuary was mainly composed of crabs, shrimps, amphipods, isopods, mysids, polychaetes and fishes, all of them occurring in more than 5% of the digestive tract contents of both species (Fig. 2). Therefore, a high dietary overlap between the species was found (0.82) and generally no significant variations were detected when comparing the consumption of the most important prey groups by the two species ($G_w < 3.84$; $df = 1$; $p > 0.05$). However, that was not the case for polychaetes ($G_w = 20.68$; $df = 1$; $p < 0.001$) and shrimps ($G_w = 4.45$; $df = 1$; $p < 0.05$). In fact, although crabs constituted preferred prey for both species, polychaetes were also a very important food item for the European eel but not for the Lusitanian toadfish, in contrast to shrimps which were more important for toadfish (Fig. 2). The consumption of amphipods and mysids decreased with the size of toadfishes, being gradually replaced by more robust prey like shrimps, crabs and fishes in the diet of larger individuals. As a consequence, the dietary overlap between eels and larger toadfishes ($TL > 170$ mm) was lower (0.71) than when the other size classes of this species were considered (0.86 for small and 0.87 for

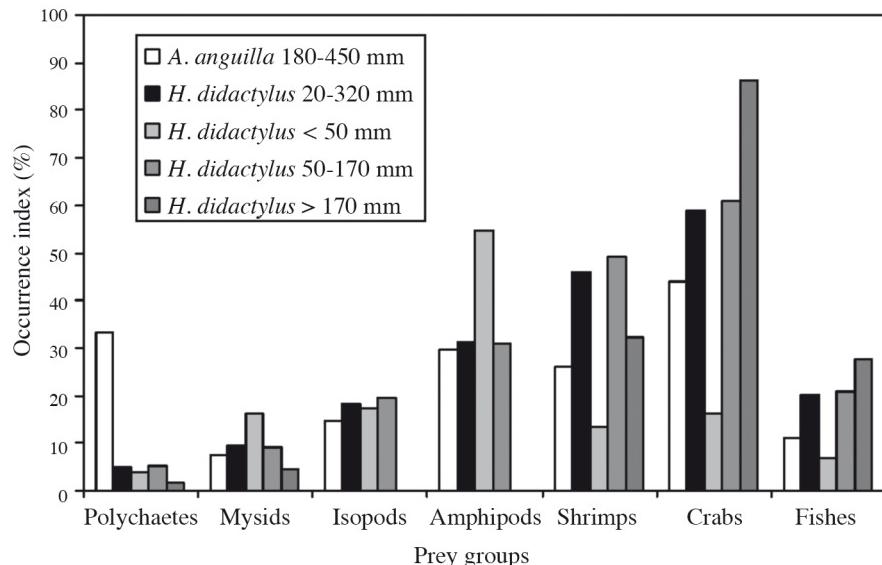


Figure 2. - Values of the index of occurrence of the most important prey groups consumed by *Anguilla anguilla* and *Halobatrachus didactylus* in the Mira estuary. [Valeurs de l'indice d'occurrence des principales proies consommées par *A. anguilla* et *H. didactylus*.]

medium individuals).

Glass eels and yellow eels represented 1.8% and 1.2% of *H. didactylus* fish consumption, respectively. On the contrary, eels were not found to prey on toadfish.

DISCUSSION

The density of *H. didactylus* was highest in the middle-lower zone of the Mira estuary where it accounted for about 100 ind.ha⁻¹. The advantage of being a large and robust species combined with the optimal thermal conditions for reproduction found in the middle estuary seem to be responsible for the dominance of *H. didactylus* in the fish assemblage of that zone (Costa, 2004). The reduced water temperature near the river mouth during the spawning period, which occurs in spring and early summer (Palazón-Fernández *et al.*, 2001; Costa and Costa, 2002), seems to be unfavourable for the species' reproductive success and may account for the downstream smooth decreasing trend in its abundance (Costa and Costa, 2002). Additionally, the difficulty of concealment in sediments of vegetated areas (Costa, 2004) is likely to be responsible for the important reduction in the abundance of the Lusitanian toadfish in *Zostera* spp. beds, especially in the intertidal zone (*Zostera noltii*), where the physiological stress increases. According to the results obtained by Ribeiro *et al.* (2006) for Ria Formosa, an open brackish lagoon in the south coast of Portugal, these estuarine vegetated areas may act mainly as nursery grounds for juveniles of this species. In the Mira upper estuary *H. didactylus* becomes much scarcer as a result of the sharp decrease in salinity in that region, as the upper limit of this species distribution in estuaries is set by the influence of freshwater (Costa and Costa,

2002). This pattern of distribution of *H. didactylus* in the Mira estuary is in agreement with the general pattern observed in similar systems (Costa and Costa, 2002; Costa, 2004).

This study showed that in the Mira estuary the abundance of the European eel is negatively related to that of the Lusitanian toadfish. In fact, in this water basin European eel density increases in an upstream direction, particularly in freshwater, which is in opposition with the pattern of abundance of the Lusitanian toadfish and is contrary to the pattern of distribution generally observed for anguillids in other systems, where the peak of abundance occurs in the middle estuary (e.g. Sloane 1984; Naismith and Knights 1993; Tzeng *et al.* 1995; Costa *et al.*, 2008). Furthermore, in the lower estuary *A. anguilla* was only associated with vegetated areas and especially with the intertidal *Z. noltii* beds, where *H. didactylus* was almost absent. It could be argued that these habitats are only temporarily occupied by small eels during their upstream migration but the small proportion of glass eels collected in these estuarine vegetated areas cannot support this hypothesis. On the contrary, these results demonstrate a truly colonisation of *Zostera* spp. beds by the European eel. Although the available bibliography does not refer that, the exclusive presence of eels in seagrass beds in the lower estuary may reflect natural preference of *A. anguilla* for vegetated areas. However, Domingos *et al.* (2006) demonstrated that for this species the cover is especially important to small specimens avoid predation. Thus, the preferential colonisation of *Zostera* spp. beds by the European eel in this part of the estuary may be related with the high density of the Lusitanian toadfish, which possibly prevent eels from occupying bare sediments (coarse sediments in the lower estuary cannot explain the absence of eels from

those bare areas because in the upper estuary the species is abundant despite the dominance of the same type of sediments). Therefore, this pattern of distribution of *A. anguilla* towards more peripheral areas (upper reaches and *Zostera* spp. beds, especially in the intertidal area) is probably influenced by spatial segregation with *H. didactylus* as there are records of other larger or more robust fish species displacing weaker ones to less favourable areas when they occur in sympatry (e.g. Wiederholm, 1987; Hesthagen and Heggenes, 2003). In this case, the competitive disadvantage of the European eel may be amplified because the settlement of young eels in continental waters occurs after a demanding migratory process (Tesch, 2003), while the offspring of the Lusitanian toadfish hatch in the colonised areas and benefit from parental care until they have developed the anatomic characteristics of adults (Maigret and Ly, 1986). In fact, it is well documented that, apart from body size, a better condition and prior residence provide advantages in competition for space and food resources (Leimar and Enquist, 1984; Archer, 1988; Robertson, 1998; Rauch, 2006). The findings in this work are consistent with the results obtained for Ria de Alvor, a coastal lagoon located in the south of Portugal, where *H. didactylus* and *A. anguilla* also occur in sympatry and toadfishes predominate in deeper zones near the sea, whereas eels are more abundant in shallower/marginal areas (Antunes and Cunha, 1986).

In general, there were some differences in the feeding habits of *A. anguilla* and *H. didactylus* in the Mira estuary. Eels preyed more on endobenthic organisms like polychaetes, whereas toadfishes consumed a higher proportion of shrimps, which are more associated with the water column. Moreover, because the diet of the European eel in the Mira estuary was very similar to its diet in the Tagus estuary (Costa *et al.*, 1992) in a period when the Lusitanian toadfish was absent from this system due to a decrease in water temperature (Costa, 2004), there seems to be little trophic interaction between the species when they occur in sympatry. However, there was a high dietary overlap between the species in the Mira estuary, especially when only smaller ($TL \leq 170$ mm) individuals of the Lusitanian toadfish were considered, and eels represented 3.0% of fish consumed by *H. didactylus*. This is an important figure considering the low overlap in distribution between the two species and that the glass eels (the most vulnerable phase to predation) are only available for predation during a short period. Thus, besides preying upon *A. anguilla*, the Lusitanian toadfish may also exert negative effects on eels through competition for food, which can become a constraint especially in small systems with a low carrying capacity such as the Mira estuary, where the density and individual growth of *H. didactylus* are negatively correlated (Costa, 2004). In such circumstances, even the high trophic plasticity of the European eel (Tesch, 2003) seems to be insufficient to enable a diversification of its diet (which remains similar in the pres-

ence or absence of *H. didactylus*) and the ingestion of enough food to assure the energetic needs of the individuals (if the system has limited food resources for *H. didactylus* the situation should be worse for *A. anguilla*, a sub-dominant species with similar feeding habits). Therefore, predation by the Lusitanian toadfish combined with competition for food can help to explain the peripheral distribution of the European eel in the Mira river basin and suggest that in ecosystems where both species are sympatric their trophic interaction may contribute to a detrimental effect on the distribution and abundance of eels. The results from this investigation are consistent with Moriarty's (1987) suggestion that the scarcity of eels in areas with higher marine influence may be related to the avoidance of predators and competitors for space and food.

Both *A. anguilla* and *H. didactylus* are benthic fish with burrowing and concealment habits which show a high dietary overlap in the Mira estuary, a system with limited food resources. Moreover, the Lusitanian toadfish preys on glass and yellow eels, which together with its dominance in the estuary may contribute to push eels to peripheral areas upstream (upper estuary and freshwater) and downstream (*Zostera* spp. beds) and consequently to their mutual exclusion. This spatial segregation, which seems to be extended to other brackish water systems, decreases the risk of predation of eels and the potential competition for food but reduces habitat availability for the European eel and may have serious consequences on a population that has already been subjected to an extensive loss of habitat induced by human influence and a drastic recruitment decline in recent years (Feunteun, 2002; Dekker, 2003; Domingos, 2003). The situation may become even more unfavourable to the European eel because subtropical species like the Lusitanian toadfish may spread northward as a result of rising temperatures caused by climatic change (Cabral *et al.*, 2001).

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